

POSTNATAL DEVELOPMENT IN *PEROMYSCUS*
MANICULATUS-*POLIONOTUS* HYBRIDS
I. DEVELOPMENTAL LANDMARKS AND
LITTER MORTALITY^{1, 2}

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ABSTRACT

Newborn laboratory hybrids of *Peromyscus maniculatus* and *P. polionotus* were observed daily from birth to weaning and compared with offspring of each of the parent types. The F₁ hybrids were intermediate between the parent types in mean age at which pinnae unfolded, hair appeared, and eyes opened. Of the parent types, the pinnae of *P. polionotus* opened one day later than *P. maniculatus*. Hybrid offspring were less viable than the parent types, with a mortality peak noted during the second postnatal week.

Previous studies of development of young mice of the North American cricetid genus *Peromyscus* have been conducted by several workers. Svihla (1932) surveyed postnatal development in five species, including several races of the species *P. maniculatus*. McCabe and Blanchard (1950) conducted rather extensive comparative studies of the development of *P. maniculatus* and two other species. King (1958) investigated several aspects of development in the *P. maniculatus* subspecies *bairdii* and *gracilis* in connection with his studies of the behavior in these forms. All of these studies have included data on the age of appearance of various developmental landmarks, such as the time at which the eyes opened or pigmentation of the dorsum occurs. However, descriptions of the developmental characteristics of interspecific hybrids previously have not been available. Likewise, there are no detailed reports of postnatal mortality in this genus. In view of this deficiency and the widespread interest in genetics and speciation in *Peromyscus*, studies of this nature were initiated to explore the effects of hybridity upon postnatal development. It was thought that any evidence of disruption of expected developmental processes or inviability of young hybrids might be of significance in the origin of physiological isolation between closely allied species.

STOCKS AND METHODS

Peromyscus maniculatus bairdii (prairie deer mouse) and *P. polionotus subgriseus* (oldfield mouse) were chosen for this study, since the ability of these species to interbreed in captivity to a limited extent was known (Dice, 1933; Watson, 1942; Liu, 1953) and stocks of these mice were available at the genetics laboratory of The Ohio State University Department of Zoology and Entomology, where this study was conducted.

Several classes of matings were established. These included reciprocal crosses between the parent species, crosses among F₁ from the female *P. maniculatus* × male *P. polionotus* cross, hereafter designated MPF₁, and reciprocal backcrosses between MPF₁ and the parent species. At least five matings of each type were attempted.

Daily examinations were made of litters from birth to weaning. The age at which pinnae unfolded, at which hair exclusive of vibrissae could first be detected upon gross examination, and at which eyes first opened were noted. A daily

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record was maintained of litter mortality and of significant features concerning the young mice, such as eczema, striking variations in pelage or state of health. Note was also taken of newborn litters successfully nursing and of any marked parental neglect or defensiveness. Such observations were made on all the hybrid classes of matings and upon sample matings of each of the parental types.

In statistical analyses of the data, "Students' *t*" tests were employed to detect any significant differences between means of the various classes of mice. Comparisons were made between *P. maniculatus* and *P. polionotus* and also between reciprocal backcrosses. Statistical comparisons of the MPF₁ or F₂ with either parent type were not performed, since, in general, the means fell between the parental values as expected. Samples of offspring from the reciprocal cross, female *P. polionotus* × male *P. maniculatus* were too small to be of value in statistical comparisons.

RESULTS

The mean age in days, based upon the means for each litter, at which pinnae evolved, at which hair first appeared, and at which the eyes first opened are given in Table 1. Pinnae generally unfolded the second or third day in all types. On

TABLE 1
Mean age in days of appearance of developmental landmarks taken by litter

Type mating			Number of litters	Pinnae unfold		Number of litters	Appearance primary hair		Number of litters	Eyes open	
Female	Male			Mean	S.E.		Mean	S.E.		Mean	S.E.
M	×	M	27	1.88±	.14	25	4.60±	.19	24	13.21±	.28
P	×	P	53	2.98±	.10	58	4.78±	.12	57	13.74±	.17
M	×	P	54	2.61±	.09	51	4.71±	.15	54	13.35±	.19
P	×	M	4	1.25±	.25	5	4.00±	.32	3	13.33±	.33
MPF ₁	×	MPF ₁	25	2.24±	.18	23	4.39±	.22	25	13.04±	.25
M	×	MPF ₁	34	2.55±	.18	22	5.00±	.17	31	13.23±	.22
MPF ₁	×	M	27	2.07±	.13	23	4.43±	.14	18	13.61±	.30
P	×	MPF ₁	5	2.60±	.24	6	4.50±	.43	7	14.14±	.40
MPF ₁	×	P	10	2.40±	.27	6	4.33±	.42	5	13.20±	.58

MPF₁ designates progeny from female *maniculatus* × male *polionotus*.

M designates *P. maniculatus*.

P designates *P. polionotus*.

the average, pinnae of *P. polionotus* projected approximately one day later than *P. maniculatus* a significant difference ($P < .001$). The difference between the mean time of pinnae unfolding in reciprocal backcrosses of MPF₁ to *P. maniculatus* was also significant at the .001 level, with pinnae unfolding slightly later when *P. maniculatus* was the female in the cross. The mean age of pinnae opening in the MPF₁ and MPF₂ fell between the means of the parental types.

There was no significant difference between *P. maniculatus* and *P. polionotus* in the mean age of appearance of first hair and first eyes opening, although the mean age in *P. polionotus* was later than in *P. maniculatus* in both instances. Differences between the reciprocal backcrosses to *P. maniculatus* in the first appearance of hair were barely significant at the .05 level based on total litters. However, this analysis did not take into account the non-independence of the litters; thus, the difference is doubtful. The means of the MPF₁ hybrids fell between those of the parental classes in both the age of hair appearance and eyes opening.

In both species and all hybrids, the dorsum was pigmented by the second day, but rarely by the end of the first day.

A tabulation of the absolute and proportional litter mortality by two-day periods is presented in Table 2. All categories of matings exhibited a high initial litter mortality, which is lumped into a pre-five-day period. Most of this occurred during the first two days and was the result of unattended young, many of which were devoured by the parents. Cannibalism was particularly frequent among *P. polionotus*. Young which survived past four days had a high probability of

TABLE 2
Litter mortality from birth to weaning
Upper entry: Absolute mortality
Lower entry: Proportion mortality

Cross	Days of Age	Pre-5	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22
M × M		115 .804	6 .041	3 .021	6 .042	3 .021	2 .014	1 .007	3 .021	3 .021	1 .007
P × P		413 .877	30 .064	6 .013	1 .002	4 .008	10 .021	0	5 .011	0	2 .004
M × P		103 .505	8 .039	14 .069	32 .157	18 .088	15 .074	3 .015	6 .029	4 .020	1 .005
P × M		22 .786	2 .071	0	1 .036	1 .036	2 .071	0	0	0	0
MPF ₁ × MPF ₁		66 .759	5 .057	1 .011	0	2 .023	3 .034	5 .057	2 .023	1 .011	2 .023
M × MPF ₁		47 .588	5 .063	4 .050	2 .025	4 .050	2 .025	5 .063	2 .025	3 .038	6 .075
MPF ₁ × M		33 .524	2 .032	6 .095	0	7 .111	2 .032	7 .111	3 .048	2 .032	1 .016

M designates *P. maniculatus*.

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MPF₁ designates progeny from female *maniculatus* × male *polionotus*.

living to weaning age, although among the MPF₁ much of the mortality occurred after five days of age. Figure 1 graphically presents the proportional litter mortality. An increase in litter mortality in the MPF₁ is depicted during the second postnatal week. This rise is not apparent in the *inter se* parental crosses nor in the MPF₂. Scattered deaths in several litters of different matings accounted for this increase; thus, there is some indication that the mortality is related to hybridity of genotype. A chi-square contingency test, grouping the mortality by week and comparing the MPF₁ with the combined progeny of the other classes, indicated that the increased death rate of MPF₁ during the second week largely accounted for a significant chi-square value ($P < .001$). Loss of entire litters due to juvenile diarrhea or other causes accounted for certain high mortality values in the backcrosses.

Pronounced scurf was noted in many young, especially at the age of hair appearance. A certain amount of scaling is normal in young deer mice at this age, but in some it was severe and persisted for several days. Some scurfy young were noted among the offspring of all categories of matings, but they appeared more commonly in certain matings. Subsequent litters from the same matings sometimes differed in the degree of scurfing. However, no correlation between severe scurf and mating category was noted.

Sores and scabs, especially in the sternal region, appeared on certain young. These sternal lesions were noted in progeny from two of the MPF₁ × MPF₁

matings, one of the female *P. polionotus* × male MPF₁, and one of the female *P. polionotus* × male *P. maniculatus*. In the first three instances, more than one young in different litters showed the sores. Such sores appeared about four or five days of age and were generally healed by fifteen days of age. These lesions did not appear to be bites or injuries from the parents, but had a characteristic appearance not seen elsewhere.

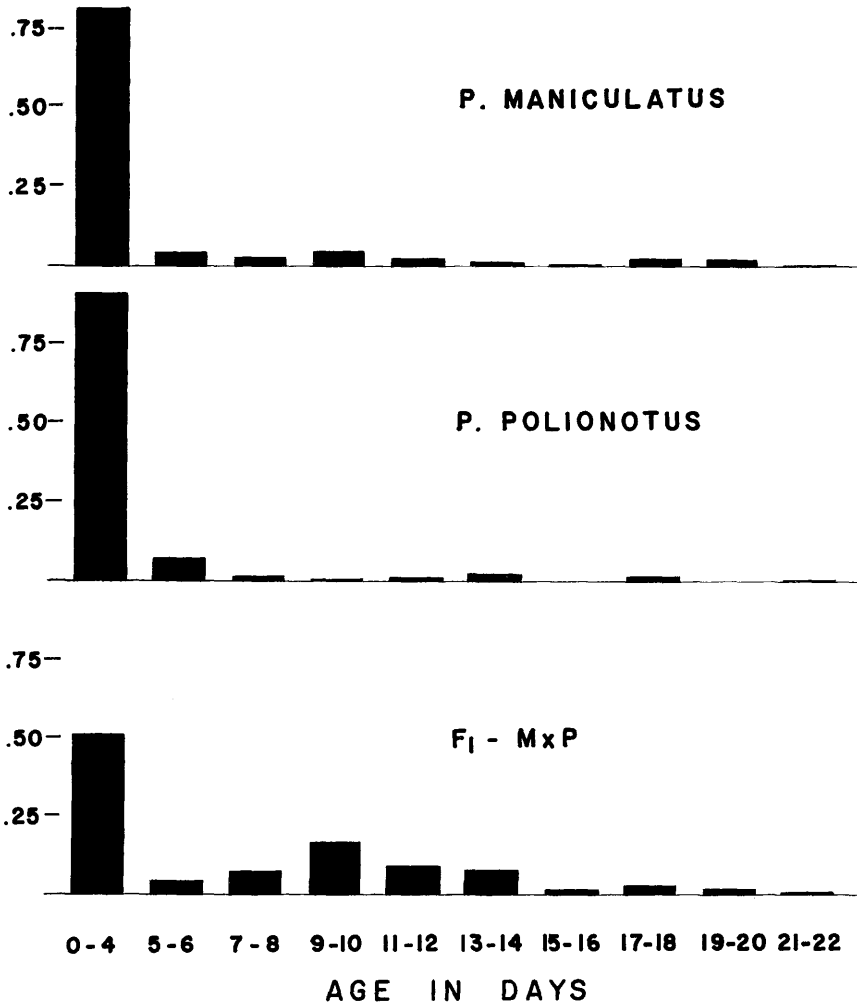


FIGURE 1. Proportional litter mortality in parent species and *F₁* hybrids.

DISCUSSION

Relatively few of the observations in this study are directly comparable to those of previous investigations, since in most instances other workers have chosen different races of deermice, and these may vary widely from one to another in onset time of developmental landmarks. In general, the observation of Svihla (1932) held true here, that the pinnae unfold after the first day but not later than the third day, following birth in members of the subgenus *Peromyscus*, of which *P. maniculatus* and *P. polionotus* are members. A more direct comparison can

be made in the case of the time at which eyes open, since both Svihla (1932) and King (1958) made observations on the race *P. maniculatus bairdii*. Svihla found the mean time for eyes opening, based on six litters, to be $13.67 \pm .38$ days, while King found the mean age in a sample of the same race to be 12.1 days. The findings here compare favorably, in that eyes in *P. m. bairdii* opened at a mean age of $13.21 \pm .28$ days.

Since there was no significant difference in the age of appearance of the developmental landmarks in the two parent types, except in the case of pinnae unfolding, no departure from the parental values in the hybrids would be expected under a multifactoral quantitative genetic model. This generally proved to be the case. Only in the reciprocal backcrosses of the MPF_1 to *P. maniculatus* was a significant difference noted in the time of pinnae unfolding and perhaps in age of pelage appearance. In this case, a maternal factor may have accounted for the difference. The data suggest that MPF_1 mother produces young which develop at a slightly accelerated rate, compared with the progeny from the reciprocal cross. Whether this can be related to reciprocal differences in size inheritance observed in this cross (Dawson, 1965) is conjectural.

The increased mortality of the MPF_1 young during the second postnatal week is sufficient to reduce litter size at weaning to a level below that of the parental types, although litter size at birth is intermediate. Factors which affect litter survival may have relevance in physiological isolation between related species, since the hybrid has a reduced probability of survival to weaning age.

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